EARLY EOCENE INSECTIVORES (MAMMALIA) FROM THE PEOPLE'S REPUBLIC OF MONGOLIA

by D. E. RUSSELL *and* D. DASHZEVEG

ABSTRACT. The early Eocene insectivores of the Tsagan-Khushu locality in Mongolia are described. Two new genera and species of Nyctitheriidae, *Bumbanius rarus* and *Oedolius perexiguus*, and two new genera and species of Palaeoryctidae, *Naranius infrequens* and *Tsaganius ambiguus* are described and compared. A pantolestid similar to *Palaeosinopa* and an unidentified form bearing a resemblance to *Hyracolestes* are also discussed. This study indicates that the early Eocene insectivores of Mongolia were not strongly endemic and probably participated in the Holarctic faunal distribution through Europe and North America.

THE early Eocene part of the Mongolian Naran-Bulak Formation, the Bumban Member, has furnished a varied fauna. Elements of this assemblage have been described (Dashzeveg, 1976, 1977, 1979*a*, *b*; Dashzeveg and McKenna 1977) in articles that establish its relationship to the Holarctic fauna known in the Ypresian of Europe and the Wasatchian of North America. An analysis of the faunas of the Naran-Bulak Formation was presented by Dashzeveg (1982). Continuing research and screen-washing techniques by one of us (D. D.) have produced the small mammals described below.

The material was collected from two quarries in the Bumban Member at Tsagan-Khushu (see text-figs. 1, 2). At Quarry I the fossiliferous sediments consist of lenses of sandy gravel conformably overlying the compact green clays of the Naran Member. Tapiroids (*Homogalax*), hyracotheres (*Hyracotherium*), hyopsodont condylarths (*Hyopsodus*), eurymylids (*Gomphos*), rodents (Ctenodactylidae), primates (*Altanius*), and lizards, birds, small gastropods, and ostracods have been found. Quarry II, also situated near the limit of the Naran and Bumban Members, was discovered 250 m south of Quarry I. Again, the fossiliferous sediments consist of sandstone and gravel; rodents, condylarths, primates, tapiroids, and other groups have been recovered from here, as well as salamander and bird remains.

The specimens described here (and measured in millimetres) are the property of the Mongolian Academy of Sciences, Institute of Geology, Palaeontology and Stratigraphy Section and bear the catalogue numbers of the latter (prefixed PSS).

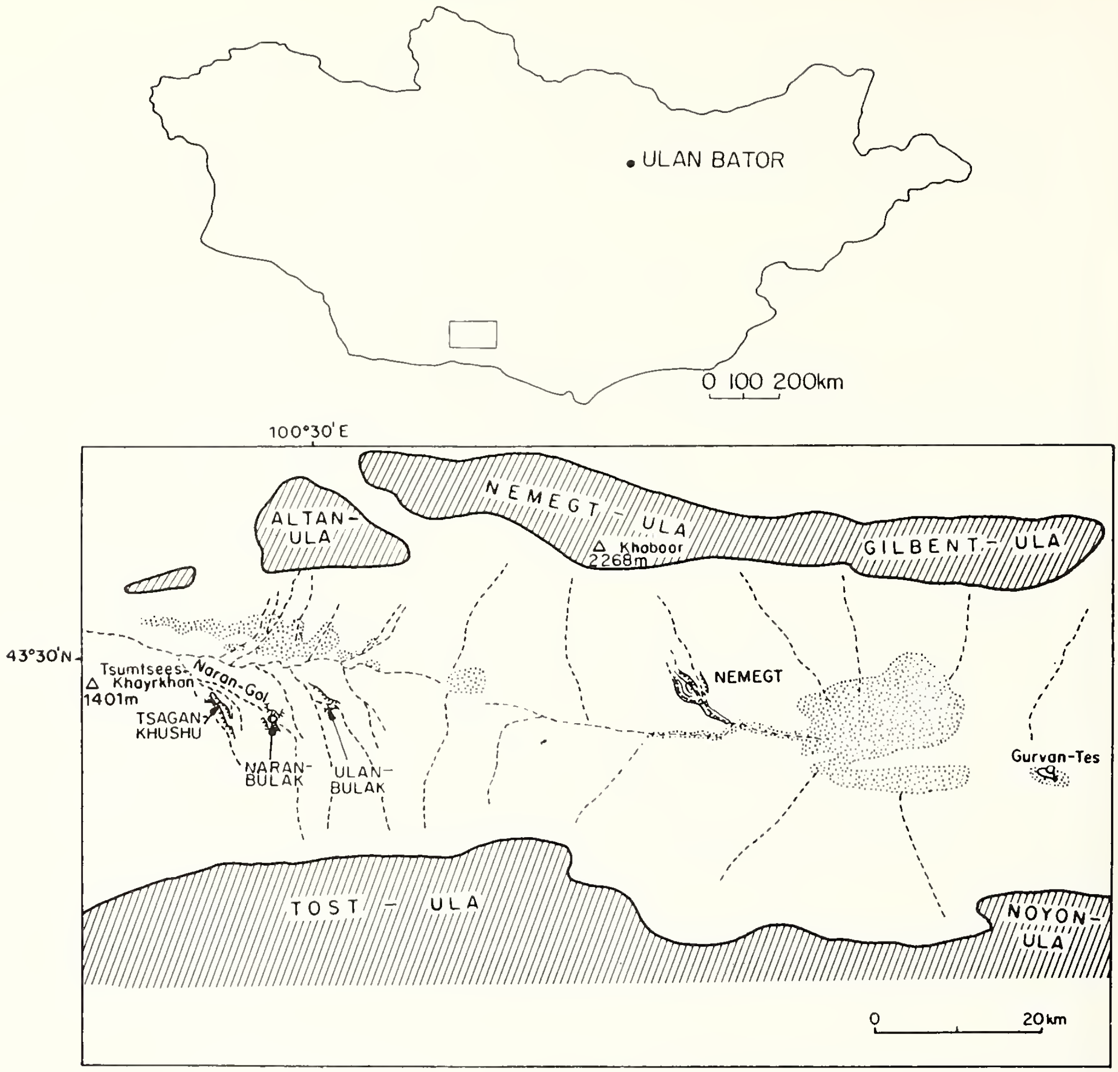
SYSTEMATIC PALAEONTOLOGY

Order LIPOTYPHLA Haeckel, 1866
Family NYCTITHERIIDAE Simpson, 1928
Bumbanius gen. nov.

Type species. *Bumbanius rarus* n. sp.

Diagnosis. Dental formula ?-?-4-3. P/2 and P/3 unreduced and biradicular; P/2 subequal to P/3. P/4 with large low paraconid, large high metaconid, and small talonid slightly basined lingually, with single median cusp at extremity of anteroposteriorly directed cristid obliqua. M/1–M/3 all approximately same length; cusps rather massive; paraconid large and low situated; strong anterocingulum; metaconid largest trigonid cusp; oblique groove present between summit of metaconid and anterior extremity of cristid obliqua; wide basined talonid; hypoconid biggest (and highest) talonid cusp, with hypoconulid intermediate and entoconid smallest; entoconid situated obliquely

[Palaeontology, Vol. 29, Part 2, 1986, pp. 269–291.]



TEXT-FIG. 1. Sketch map of the Nemegt Basin, Mongolian People's Republic, showing the situation of Tsagan-Khushu and the other Palaeogene localities of Naran-Bulak and Ulan-Bulak (modified from Gradzinski *et al.* 1969), with the region indicated in a general map of Mongolia.

at posterolingual corner of talonid, slightly posterior with respect to hypoconid; M/3 hypoconulid short but prominent.

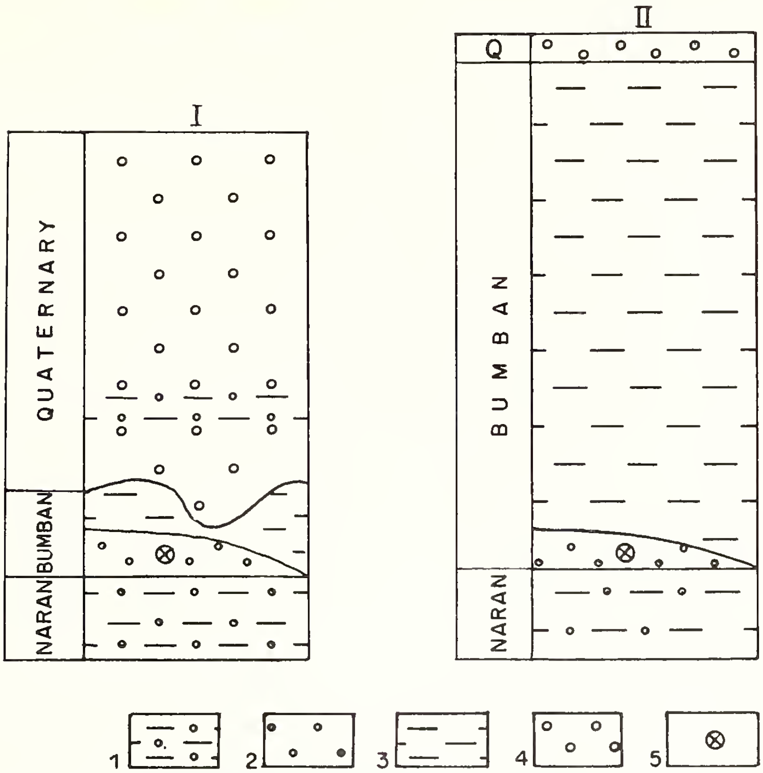
Etymology. Named for the Bumban Member of the Naran-Bulak Formation.

Bumbanius rarus sp. nov.

Text-figs. 3 and 4

Holotype. Specimen PSS 20-96, right mandibular fragment with M/1–M/3.

Referred material. PSS 20-88, right mandibular fragment with P/4 and alveoli of P/2–P/3; PSS 20-66, right



TEXT-FIG. 2. Stratigraphic sections showing the position of the fossiliferous deposit within the Naran-Bulak Formation at the outcrops of Tsagan-Khushu. I, at Quarry I; II, at Quarry II; 1, green clay of the Naran Member; 2, fossiliferous lenses of reddish sand and sandstone; 3, red clay of the Bumban Member; 4, Quaternary sands and gravels; 5, fossil locality.

mandibular fragment with P/4–M/1; PSS 20-69, left mandibular fragment with M/2; PSS 20-131, right mandibular fragment with M/3; PSS 20-57, left maxillary with M1/–M2/ and roots of P3/–P4/ and M3/; PSS 20-68, left M2/.

Locality and horizon. Tsagan-Khushu, Nemegt Basin, People's Republic of Mongolia; Naran-Bulak Formation, Bumban Member, Quarry I (PSS 20-66, PSS 20-69, PSS 20-57) and Quarry II (PSS 20-88, PSS 20-96).

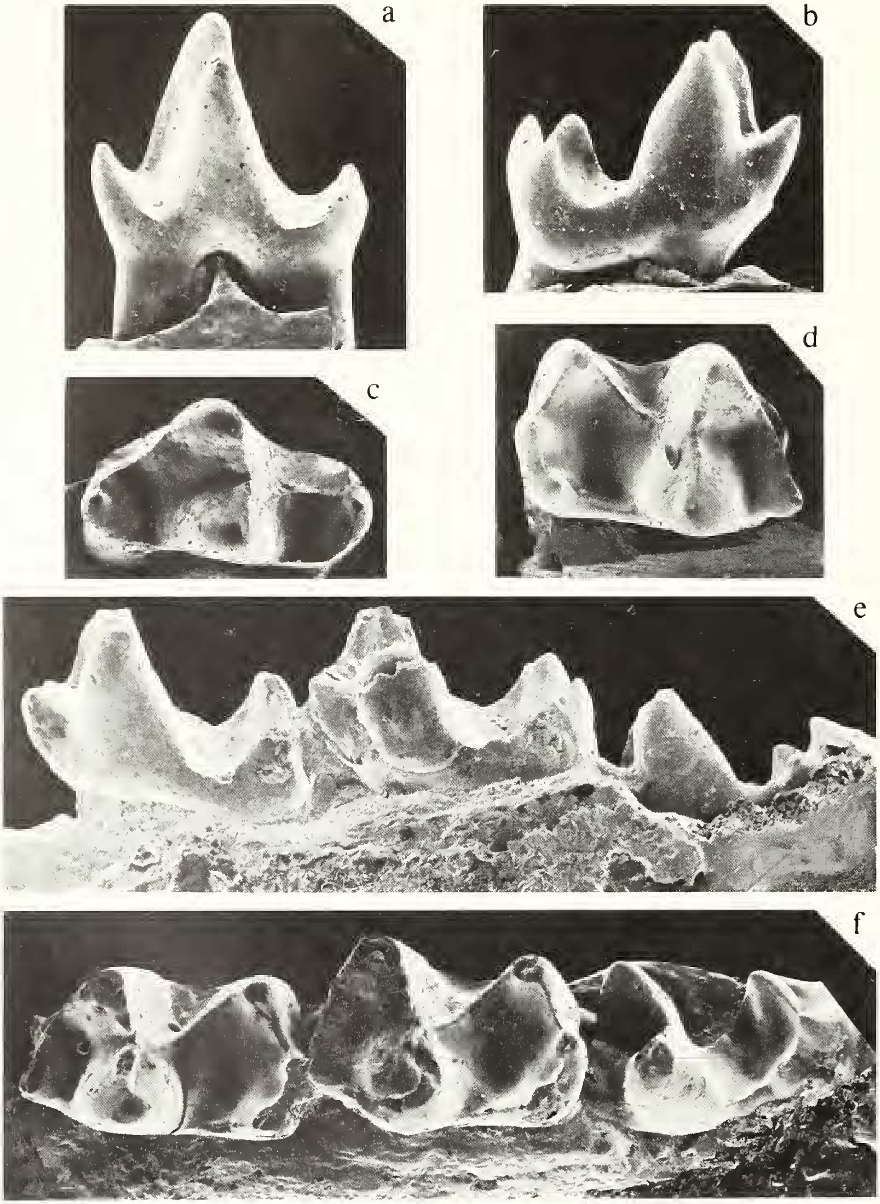
Age and distribution. Early Eocene of the Naran-Bulak Formation at Tsagan-Khushu.

Diagnosis. As for genus.

Etymology. rarus, Latin; so named because of its relative infrequency in the fauna.

Description. The mandible is long and low and is preserved (in composite) between the posterior alveolus of P/1 and the level of M/3; a single mental foramen is visible below the posterior root of P/3 and the symphysis extends to below the anterior part of P/2. P/2 and P/3 are not known, but from the ridges separating the 4 empty alveoli in front of P/4 both of these teeth must have possessed 2 roots; the crown length of each was not much less than that of P/4. With respect to the vertical axis of the mandible, the crowns of P/4–M/3 are tilted lingually; with respect to the vertical plane of the symphysis, the teeth are vertical and the mandible is tipped labially.

P/4 (text-fig. 3*a*, *c*) is dominated by a high, narrow protoconid; the well-detached metaconid is nearly as high as the protoconid; a vertical anterior crest on the protoconid joins at its base a large, rather transverse paraconid, situated low on the crown. A short anterocingulum is present. The talonid is short and basined only lingually, being divided by an anteroposteriorly directed cristid obliqua. The posterolingual limiting crest of the talonid is variably developed, but no cusp is formed; only a single median cuspule is present at the extremity of the cristid obliqua.



TEXT-FIG. 3. *Bumbanius rarus* gen. et sp. nov. *a* and *c*, PSS 20-88, right P/4; *a*, lingual view; *c*, occlusal view, ×20. *b* and *d*, PSS 20-69, left M/2; *b*, lingual view; *d*, occlusal view, ×20. *e* and *f*, PSS 20-96, right M/1–M/3, holotype; *e*, lingual view; *f*, occlusal view, ×20. All specimens are from Tsagan-Khushu, Naran-Bulak Formation, Bumban Member, MPR, and are housed in the Institute of Geology, Ulan Bator.

The molar trigonids (text-fig. 3*b–f*) are of moderate height; a moderately strong but crestiform paraconid, situated well below the metaconid, projects anteriorly and connects with the sharp anterior vertical crest of the protoconid. The trigonid basin is well developed and closed lingually to a variable degree according to the tooth in the molar series. The talonid is long and broadly basined; the talonid cusps decrease in size from the hypoconid to the entoconid; the hypoconulid and entoconid are joined by a higher crest than that between the hypoconid and the hypoconulid. The anterocingulum is consistently present and (in one out of three specimens) can continue labially below the protoconid; postero-cingular development is very slight.

A left maxillary, PSS 20-57 (text-fig. 4), with M1/–M2/ and the roots of P3/–P4/ and M3/ is considered as possibly referable to *B. rarus*. It occludes fairly well with the only left molar in the collection, PSS 20-69. From the roots of P3/ this tooth was principally elongate with little lingual expansion of the protocone. Apart from the evident fact that the P4/ was an approximately triangular tooth, little can be said of it except that it was proportionally similar to the P4/ of *Leptacodon*: narrow but rounded lingually, with a metastylar lobe considerably longer and larger than that of the parastyle.

TEXT-FIG. 4. *Bumbanius rarus* gen. et sp. nov. PSS 20–57, left M1/–M2/, occlusal view, ×20. From Tsagan-Khushu, Naran-Bulak Formation, Bumban Member, MPR.

M1/ and M/2 are transversely elongate with an anteriorly directed parastyle, a larger metastylar lobe, and complete absence of a mesostyle. The labial border is gently indented; slight basining occurs labial to the metacone. The paracone is considerably higher and more voluminous than the metacone; they are well separated at their base. A sharp crest connects the metastyle and the metacone; a slighter, labially directed crest extends between the summit of the paracone and a point posterior to the parastyle. The conules are well developed, with the paraconule being the larger and higher. Crests diverge from the paraconule to join the lingual base of the paracone and the anterior tip of the parastyle. The premetaconule crista is rather weak and extends to the anterolingual side of the metacone; the postmetaconule crista extends posterolingually at the base of the metacone and disappears before reaching the metastyle. A deep trigon basin is formed between and labial with respect to the conules. The protocone is as high as the paracone and has a long sloping lingual surface. Far below the summit of the protocone a small and somewhat cuspate hypocone occurs at the lingual extremity of a strong posterior cingulum. The anterior cingulum is short and weak. From the position of its roots, M3/ was a triangular tooth with a strongly sloping posterolabial border.

A second specimen of the upper dentition, PSS 20-68, appears to be an upper M2/ referable to *B. rarus*. It has been damaged labially, but size and most of its features are compatible. Some differences translate individual variation within the species and the specimen is of interest for this reason. Cingular development is stronger, with the hypoconal shelf being wider; both it and the antero-cingulum extend farther lingually than on the tooth of PSS 20-57. Also, the premetaconule crest is more pronounced, as were, apparently, the conules.

Measurements.

		Length	Width
PSS 20-57:	M1/	2·15	2·45
	M2/	2·35	2·9
PSS 20-66:	P/4	1·8 est.	1·05
	M/1	1·8 est.	1·2
PSS 20-69:	M/2	1·9	1·25
PSS 20-88:	P/4	1·9	1·0
PSS 20-96:	M/1	1·9	1·2
	M/2	1·9	1·2
	M/3	1·9	1·2
PSS 20-131:	M3/	1·85 est.	1·2

Comparisons. P/4 differs from that of *Leptacodon* (only *L. tener* and *L catalus*) in having a larger paraconid and metaconid and in having an anteroposteriorly directed cristid obliqua. M/1 differs from that of *Leptacodon* in having a more anteriorly directed paraconid. M/1–M/3 differ from those of *Leptacodon* in the placement of the entoconid slightly posterior with respect to the hypoconid and situated obliquely at the posterolingual corner of the talonid; it is separated by a U-shaped notch (not a V) from the trigonid. Also, the hypoconulid is higher and slightly larger than the entoconid. *B. rarus* is bigger than *Leptacodon* but very close in size to *Praolestes*.

Apart from size *Praolestes* also shows a similarity that could translate familial affinity; on the generic level, however, it is very distinct. The P/4 of *Bumbanius* differs in being longer and lower with its paraconid larger and situated much lower on the crown, its metaconid larger and relatively much higher above the top of the paraconid, and it differs in the point of contact of its cristid obliqua (which is anteroposteriorly oriented), far below the median side of the metaconid, being more labial. However, in occlusal view, for example, the morphology of both the trigonid and talonid in the two forms follows a similar pattern. The talonid appears to be longer in *Bumbanius*, but it is damaged in *Praolestes*. Both animals show a well-developed oblique groove across the posterior trigonid wall of M/1.

Concerning the referred upper dentition, P3/ has a weaker lobe than in *Leptacodon* and the tooth as a whole is situated less obliquely than in the latter; in PSS 20-57 (text-fig. 4) the labial border of P3/ follows the orientation of the same border of P4/, which would indicate the presence of a wider snout.

While similar in general morphology to the upper teeth of *Leptacodon*, those of PSS 20-57 possess a higher protocone with a lingually longer sloping surface; the paracone, on the other hand, is lower and less slender; the metacones in the two taxa are more closely alike. The anterior cingulum is weaker than in the upper molars of *Leptacodon*, as is the labial cingulum labial to the paracone; in contrast, it is more basined labial to the metacone than in *Leptacodon*.

An interesting comparison can be made with the type mandible of *Adunator lehmani* from the middle(?) Palaeocene of Walbeck, Germany. The general configuration of P/4-M/3 is similar in the two forms. Differences in *B. rarus* include, for P/4, a bigger metaconid and a reduced talonid basin; for M/1-M/3, higher cusps in general, larger paraconid, a broader trigonid basin, hypoconid situated posteriorly with respect to the entoconid, entoconid smaller and hypoconulid bigger, and a narrower notch between the entoconid and the metaconid. The M/3 is relatively bigger in *Bumbanius*.

The two animals are subequal in size and share, among other features, an oblique groove parallel to the anterior end of the cristid obliqua that extends to the summit of the metaconid.

Pending knowledge of the upper teeth in *Adunator*, present evidence suggests that it and *Bumbanius* could be members of the same family.

Some resemblances in *Bumbanius* may be also noted to *Centetodon*, but as with many of the above comparisons the characters are probably mostly primitive for lipotyphlans.

Oedolius gen. nov.

Type species. Oedolius perexiguus n. sp.

Diagnosis. Dental formula 3–1–4–3. P/1 small and uniradicular. P/2 and P/3 larger than P/1, biradicular and subequal in size. P/4 with small, low paraconid, lack of metaconid, lack of talonid basining and with a single, small median cusp at posterior extremity of tooth. M/1–M/3 all approximately same length (or, M/3 the longest); cusps slender and moderately high; paraconid low but prominent; strong anterocingulum; protoconid and metaconid subequal; strong oblique groove present below summit of metaconid, emphasized by anterior part of cristid obliqua. Molars relatively narrow; hypoconid most voluminous talonid cusp but equalled in height (or exceeded) by hypoconulid; entoconid small, situated obliquely at posterolingual corner of talonid, slightly posterior with respect to hypoconid. M/3 hypoconulid short to moderately developed but prominent.

Etymology. Oedolius, from the name of the locality of Oedol, not far from Naran-Bulak.

Oedolius perexiguus sp. nov.

Text-fig. 5

Holotype. Specimen PSS 20-103, left mandibular fragment with M/1–M/2 and talonid of P/4.

Referred material. PSS 20-71, left mandibular fragment with bases of M/2–M/3; PSS 20-74, right mandibular fragment with M/2; PSS 20-76, left mandibular fragment with damaged P/4–M/2 and alveoli of P/1–P/3; PSS 20-77, right mandibular fragment with P/4 and alveoli of P/1–P/3; PSS 20-78, right mandibular fragment with talonid of M/3; PSS 20-80, left mandibular fragment with M/2–M/3; PSS 20-86, left mandibular fragment with damaged M/2–M/3 and talonid of M/1; PSS 20-87, left mandibular fragment with M/3; PSS 20-92, right mandibular fragment with M/3 and talonid of M/2; PSS 20-94, left mandibular fragment with M/1, trigonid of M/2 and alveoli of I/1–P/4; PSS 20-102, right mandibular fragment with M/2–M/3; PSS 20-104, left mandibular fragment with P/4–M/1; PSS 20-108, right mandibular fragment with M/3; PSS 20-111, right mandibular fragment with P/4–M/1.

Locality and Horizon. Tsagan-Khushu, Nemegt Basin, People's Republic of Mongolia; Naran-Bulak Formation, Bumban Member; Quarry I (PSS 20-71, PSS 20-74, PSS 20-76, PSS 20-77, PSS 20-78, PSS 20-80, PSS 20-102, PSS 20-103, PSS 20-104) and Quarry II (PSS 20-86, PSS 20-87, PSS 20-92, PSS 20-94).

Age and distribution. Early Eocene of the Naran-Bulak Formation at Tsagan-Khushu.

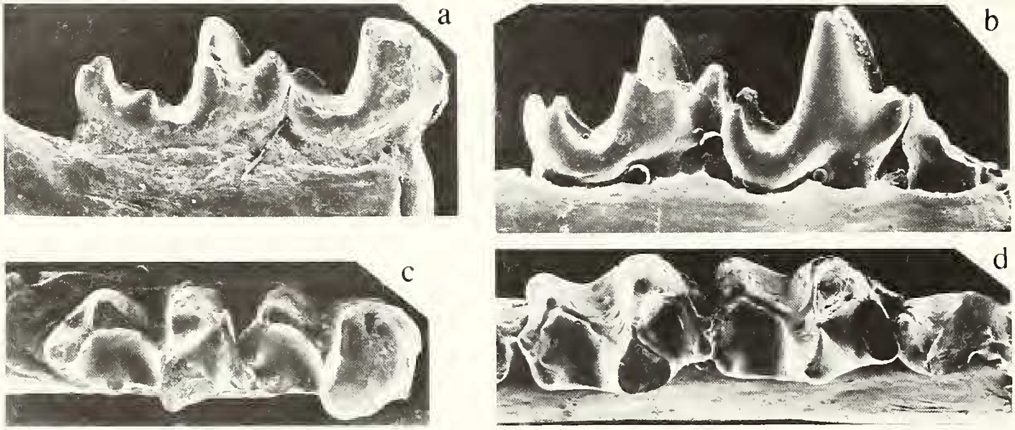
Diagnosis. As for genus.

Etymology. perexiguus, Latin; very small.

Description. The mandible is long and low; mental foramina occur below P/1 or P/2 and below the posterior side of P/3; the latter is much the smaller. The symphysis extends posteriorly to the level of P/2. The alveoli of three incisors are present, in decreasing proclivity from I/1 to I/3, and appear to have been all about the same size. From the alveolus the canine was large and single rooted; a single rooted, relatively large P/1 followed it. In PSS 20-94 the P/2 and P/3 were only slightly smaller than the P/4, but in PSS 20-76 the mandible is considerably shorter and the P/2 and P/3 are accordingly quite smaller teeth; below the premolar alveoli, however, the mandible is higher than in PSS 20-94. A third specimen, PSS 20-77, displays the tooth and jaw proportions of PSS 20-94. In all specimens the P/2 and P/3 are subequal in size. With respect to the vertical axis of the mandible the crowns of M/1–M/3 are tilted lingually; with respect to the vertical plane of the symphysis the teeth are vertical and the mandible is tipped labially.

P/4 (text-fig. 5*e*) is essentially a single cusped tooth; the paraconid is very small and situated very low on the crown and there is no metaconid. The dominant protoconid is moderately high and recurved along its anterior border. A sharp crest descends posterolingually from its summit, delimits the lingual side of the talonid and joins the single, median cuspule at the rear of the talonid; the latter is completely unbasined and slopes labially from the lingual crest.

In the molars (text-fig. 5*a*–*d*) the metaconid and protoconid are moderately high and are subequal. An anterior crest on the protoconid joins the labial base of the paraconid crest, with which it makes a rather sharp angle. The paraconid is low, about as high as the hypoconulid, and projects anteriorly. The metaconid



TEXT-FIG. 5. *Oedolius perexiguus* gen. et sp. nov. *a* and *c*, PSS 20-80, left M/2–M/3; *a*, lingual view; *c*, occlusal view, ×20. *b* and *d*, PSS 20-103, left talonid of P/4, M/1–M/2, holotype; *b*, lingual view; *d*, occlusal view, ×20. *e*, PSS 20-77, right P/4, lingual view, ×20. All specimens are from Tsagan-Khushu, Naran-Bulak Formation, Bumban Member, MPR, and are housed in the Institute of Geology, Ulan Bator.

is situated slightly posterior with respect to the protoconid and is traversed obliquely by a strong groove that extends from its summit to the labial base of the tooth. The cristid obliqua forms the lingual border of this groove and reaches high on the metaconid. The talonid is a little wider than the trigonid in M/1 and a little narrower in M/2. The hypoconid is the major cusp, with the large and medianly placed hypoconulid being subequal in height. The entoconid is the smallest of the three and is situated at the posterolingual corner of the tooth opposite the hypoconid. The talonid is deeply basined but nearly lacks a lingual wall. A broad U-shaped notch separates the entoconid and the metaconid. The hypoconulid of M/3 is narrow but prominent (in 3 out of 4 specimens). A noteworthy tongue and groove effect is achieved by the fit of the hypoconulid of the preceding tooth between the paraconid and the large anterior cingulum of the succeeding one; this is true for P/4–M/3.

Measurements.

		Length	Width
PSS 20-77:	P/4	1·25	0·55
PSS 20-94:	M/1	1·4	0·8
PSS 20-102:	M/2	1·25 est.	0·9
	M/3	1·5	0·9
PSS 20-111:	P/4*	1·25	0.55
PSS 20-74:	M/2	1·35	0·85
PSS 20-108:	M/3	1·35	0·9
PSS 20-87:	M/3	1·35	0·85
PSS 20-92:	M/3	1·3 est.	0·9
PSS 20-76:	P/4	1·0	0·55
PSS 20-104:	P/4	1·05	0·5
	M/1	1·1	0·75
PSS 20-103:	M/1	1·4	0·9
PSS 20-80:	M/2	1·4	0·9
	M/3	1·5	0·8

* Associated with M/1, but the molar is damaged and was not measured.

Comparisons. P/4 of *O. perexiguus* differs from that of *B. rarus* by its smaller paraconid, absence of metaconid, and absence of talonid basining. The molars differ by being narrower and by having more slender cusps; they differ also in the angle made by the anterior protoconid crest and the paraconid crest, by the protoconid and metaconid being subequal, by the cristid obliqua being stronger anteriorly and reaching higher on the trigonid, and by more separation of the hypoconulid and the entoconid. *Oedolius* is considerably smaller than *B. rarus*.

The P/4 (text-fig. 5*e*) of *O. perexiguus* differs from that of *Leptacodon* by its smaller paraconid, lack of metaconid, lack of talonid basining, and presence of a small, single, median talonid cusp. M/1–M/3 (text-fig. 5*a–d*) differ from those of *Leptacodon* by having a slightly thinner and higher protoconid and metaconid, by the small size and oblique placement of the entoconid, slightly posterior with respect to the hypoconid (it is anterior in *Leptacodon*), and the presence of a wide U-shaped notch between it and the metaconid, and by the relatively large size of the medianly placed (not closer to the entoconid) hypoconulid. *O. perexiguus* is about the same size as *Leptacodon* but the molars are a little narrower.

Praolestes (except for paraconid development) is much closer to *B. rarus* than to *O. perexiguus*. *Hyracolestes* is like neither, nor are the various erinaceids and dormaaliids that are known; the same can be said for the divers Chinese Palaeocene and Eocene forms that are either not comparable due to lack of lower dentitions or are dissimilar. None of the North American or European nyctitheres are as close to *O. perexiguus* as is *Leptacodon*.

Principally because of the unbasined talonid of the P/4 of *Oedolius* and its lack of a metaconid comparison with palaeoryctids and pantolestids was made. Certain points of resemblance exist with *Thylesia* among the former but nothing notable in lower molar morphology suggests a relationship to pantolestids. *Oedolius* may not fit with certitude in the concept of the Nyctitheriidae as it is presently known, but for time being, lacking a better designation, we place it in that family.

The same could be said concerning the single (and damaged) specimen of *Kashanagale* from the late Palaeocene Gashato locality (Szalay and McKenna 1971). Although the latter was described as an anagalidan, we doubt that attribution. The M/3 is shorter in *Kashanagale* than in *Bumbanius* and the cristid obliqua does not extend as high on the trigonid wall, but otherwise the morphology of M/2 and M/3 (the only teeth comparable) is quite similar.

Nyctitheriidae gen. indet.

Text-fig. 9*f*

Material. PSS 20-60, isolated right upper M1/; from Quarry I, Tsagan-Khushu.

PSS 20-60 (text-fig. 9*f*), is little worn but it has undergone postfossilization abrasion along the labial border, particularly at the extremity of the metastyle, which has been reduced also by breakage at its base. Occlusionally, nearly the total length of the metastyle is preserved, as the wear facet is intact. In basal outline the metastyle undoubtedly projected more labially than its present extension; the parastyle was also prominent but probably followed the present contour. There is wear along the anteroposterior crests of the paracone-metacone, but even taking that into account the paracone is the higher and the more tubular of the two and the metacone the more elongate anteroposteriorly; furthermore, the two cusps differ considerably in orientation, with the paracone sloping labially and the metacone being nearly vertical. The posterolingual side of the metacone forms, with the metastyle, a high shearing surface; a pronounced notch separates the two. Conules are strongly developed and situated approximately opposite each other; the paraconule is much the larger and is connected to the base of the paracone by a low crest and to the anterior side of the parastyle by the preparaconular crest. The metaconule is a sub-circular, pointed cusp and is completely isolated from both the metacone and the metastyle. A sharp indentation in the tooth outline occurs at this point, marking the limit of the hypoconal shelf, although a basal cingulum persists for a short distance along the base of the metacone. The hypoconal shelf is quite wide and supports not only a large hypocone, but also (labial with respect to the latter) a second well-developed cusp. The hypocone extends lingually beyond the level of the protocone. A short but prominent anterocingulum occurs at the anterolingual corner of the protocone and produces, with the hypocone, a squared look to the lingual basal profile of the tooth. The protocone has undergone much wear, coupled perhaps with breakage, but appears to have been originally lower than the labial cusps.

Measurements.

	Length	Width
PSS 20-60: M1/	3·1 est.	3·3 est.

Comparisons. PSS 20-60 is much larger than *Bumbanius* and *Oedolius* and incompatible with *Naranius* and *Tsaganius*. The upper teeth referred to *Bumbanius* represent a much more primitive stage of development (more transversely elongated, little shearing adaptation of the metastyle, less cingular expansion, and the anterocingulum more labially situated). No close relation is evident.

Comparison with the pantolestids and leptictids (including the Pseudorhyncocyoninae of Europe), both of which resemble to some degree PSS 20-60, was unfruitful, although a rather striking similarity was found in the upper DP4/ of *Leptictis*, even to the presence of two cusps on the hypoconal shelf. PSS 20-60 is not a deciduous tooth and is not related to the Proteutheria. In basic morphology it strongly resembles Eocene nyctitheres, but no one known form is significantly close. Despite the presence of an enlarged hypoconal lobe in the enigmatic *Sarcodon*, there is no pertinent resemblance between it and PSS 20-60. It is hoped that additional material of this taxon will be found that will enable a fuller description to be made and its affinities more precisely deduced.

A fragmentary left lower molar, PSS 20-70 (text-fig. 9*b*, *c*), with the talonid and metaconid preserved, shows characters strongly reminiscent of those of the lower molars of *B. rarus*. Its size, however, is much greater than that of the latter and thus suggests a possible affinity with the upper molar, PSS 20-60.

The Talonid of PSS 20-70, very well preserved, differs from that of the lower molars of *B. rarus* in that the hypoconulid is relatively larger, situated more medianly, and in consequence further from the entoconid. It is intermediate in height between the hypoconid (the highest and biggest) and the entoconid. The latter, also, is relatively larger, as is the hypoconid which is expanded anteriorly. The cristid obliqua differs in orientation, being directed more lingually and extends toward the summit of the metaconid emphasizing a strongly marked oblique groove. This groove and the disposition and size of the talonid cusps is consistent with our assignment of *Bumbanius*, and this specimen, to the Nyctitheriidae.

Mention should also be made of *Sarcodon* and *Hyracolestes* with respect to PSS 20-70. While there is no question of the latter being referable to *Sarcodon*, it is approximately the same size as the M/1 in AMNH 21732, the posterior trigonid wall appears to be crossed by a similar groove extending between the cristid obliqua and the summit of the metaconid, and the trigonid cusps are quite similarly distributed and have like proportions. The hypoconid was probably the highest talonid cusp in *Sarcodon* (it is broken in the single specimen known) and the hypoconulid is large and intermediate in height. But in strong contrast to PSS 20-70 the entoconid of *Sarcodon* is much closer to the hypoconulid. Apart from this feature, there is nothing in the (admittedly too meager) sample of each that would deny relationships between them.

Also furnishing speculation for affinity is the morphology of comparative parts of the first molar in *Hyracolestes*. Though the animal was smaller than that represented by PSS 20-70 and the talonid is damaged (hypoconid broken off; entoconid possibly reduced by erosion) the available evidence does suggest that, possibly, PSS 20-70 and *Hyracolestes* were related. At the same time the hypothesis arises that *Sarcodon* and *Hyracolestes* might share a common relationship.

Lipotyphla indet.

Text-fig. 6

Material. PSS 20-62, fragment of a right maxillary with M2/–M3/ and the lingual half of M1/; from Quarry I, Tsagan-Khushu.

The presence of the maxillary fragment PSS 20-62 indicates the existence of a lipotyphlan in the fauna of Tsagan-Khushu that is not represented in the collection by lower teeth. Its size is not compatible with the species of either *Bumbanius* or *Oedolius*. The heavy wear that the teeth of PSS 20-62 have undergone does not facilitate analysis.

The maxillary fragment (text-fig. 6) contains only M2/–M3/ and the lingual half of M1/; no alveoli of the

TEXT-FIG. 6. Lipotyphla indet., PSS 20-62, right M1/–M3/, occlusal view, ×20. From Tsagan-Khushu, Naran-Bulak Formation Bumban Member, MPR.

premolars remain. The teeth are transversely elongate with expansion of a posterior cingular shelf on M1/ and M2/; apparently no hypocone was developed. On M2/ the cingulum is nearly continuous across the base of the protocone. The anterior cingulum is rather weak although a marked concavity occurs between the labial limit of the cingulum and the base of the parastyle. The metaconule was apparently crestiform and included in the postprotocrista; it does not seem to have had a premetaconular crest directed toward the base of the metacone. The paraconule was probably larger and seems to have been situated more labially. Between the conules the bottom of the trigon basin is raised in a transverse, low rounded ridge that extends between the protocone and a point between the bases of the paracone and metacone. The latter cusp is considerably the smaller of the two and is inclined posteriorly; the paracone is more vertical. Both have long, sloping lingual surfaces. Wear has produced a deep, U-shaped groove between them, but originally their bases were probably much closer. Relative to the transverse diameter of the teeth their labial length is rather short. A shallow ectoflexus separates the styles in M2/ and is barely indicated in M3/. From the position of the roots the parastyle of M1/ was rather strongly directed anteriorly and the metastyle labially. In M2/ the parastyle is of moderate dimensions and is also directed anteriorly; the metastyle is directed posterolabially and is connected to the metacone by a short crest. The occlusal surface of the parastyle has been worn off. M3/ remains a rather large tooth despite the absence of a metastyle and practically no posterior cingular development.

Measurements.

		Length	Width
PSS 20-62:	M2/	1·65	2·55
	M3/	1·45	2·1

Comparisons. Due to a superficial resemblance to various Proteutheria, PSS 20-62 was compared with leptictids and pantolestids, but no affinity to these groups is evident. Palaeoryctids can also be eliminated, and among the Lipotyphla, only the Nyctitheriidae or the Geolabididae seem to show a relationship. Although not strikingly similar, PSS 20-62 most resembles *Leptacodon* among nyctitheres. Comparison with early Eocene geolabidids is not possible since upper molars have not been described for *Centetodon patratus* and *C. neashami*. The earliest available information is furnished by the middle Eocene *C. pulcher* and *C. bembicophagus*. The lingual or protoconal root is not yet, or only incipiently, divided in these species, contrasting with the condition in younger members of the genus and agreeing with the condition in PSS 20-62. *C. pulcher* upper molars are distinguished by marked but narrow pre- and postcingula and a broad labial shelf. Also, a small but distinct hypocone is present. In PSS 20-62 the labial shelf is narrower, the precingulum less developed, and the postcingulum is wider and lacking a hypocone. The upper molars of the middle Eocene *Centetodon* are more transversely elongate than those of *Leptacodon* but less than in

PSS 20-62. A slight lingual cingulum encircling the protocone occurs in PSS 20-62 and is variably present in *C. pulcher*. Although rather heavily worn, it would appear that the paracone-metacone were connate at their base in PSS 20-62, as in *Centetodon* rather than in *Leptacodon*. *Centetodon* is characterized by a flaring postmetacrista, which in PSS 20-62 is extremely short and little developed, but in *Leptacodon* it takes a different form with more of a notch between the metastyle and the metacone. A small stylocone, just posterior to the parastyle, occurs in *C. pulcher* and a suggestion of a similar feature might occur in PSS 20-62; on the other hand, it could be an artifact of wear. It does not appear in *Leptacodon*.

Comparison was also made with various dormaaliids, in particular with *Scenopagus* and *Macrocranion*, but many of the dissimilarities that separate PSS 20-62 and *Leptacodon* can also be cited for these forms. The paracone-metacone are not connate in dormaaliids and the hypocone is generally high and prominent.

The Asian *Tupaiodon*, although more likely an erinaceid, was also examined and found very different.

In conclusion, the facts tend to indicate the possible attribution of PSS 20-62 to the Geolabididae, but the evidence is still weak and uncertain. For the moment, we will refer the specimen to Lipotyphla indet.

Order PROTEUTHERIA
Family PALAEORYCTIDAE (Winge, 1917) Simpson, 1931
Subfamily DIDELPHODONTINAE Matthew, 1918
Naranius gen. nov.

Type species. *Naranius infrequens* n. sp.

Diagnosis. Dental formula 3-1-4-3. P/1 uniradicular, P/2 and P/3 small, biradicular, and subequal in size. P/4 with minute basal paraconid, no anterocingulum, no metaconid, no talonid basining but talonid traversed medianly by a crest with a moderately developed cusp at its posterior extremity. M/1 and M/2 of approximately same length; M/3 longest; cusps moderately slender and moderately high; paraconid relatively high and small; strong anterocingulum; protoconid and metaconid subequal; no oblique groove on posterior surface of metaconid; cristid obliqua contact low on trigonid and slightly labial with respect to protoconid-metaconid notch; hypoconid biggest (and highest) talonid cusp, with hypoconulid intermediate and entoconid smallest; entoconid situated at posterolingual corner of talonid, opposite hypoconid. M/3 with long, narrow talonid and large prominent hypoconulid.

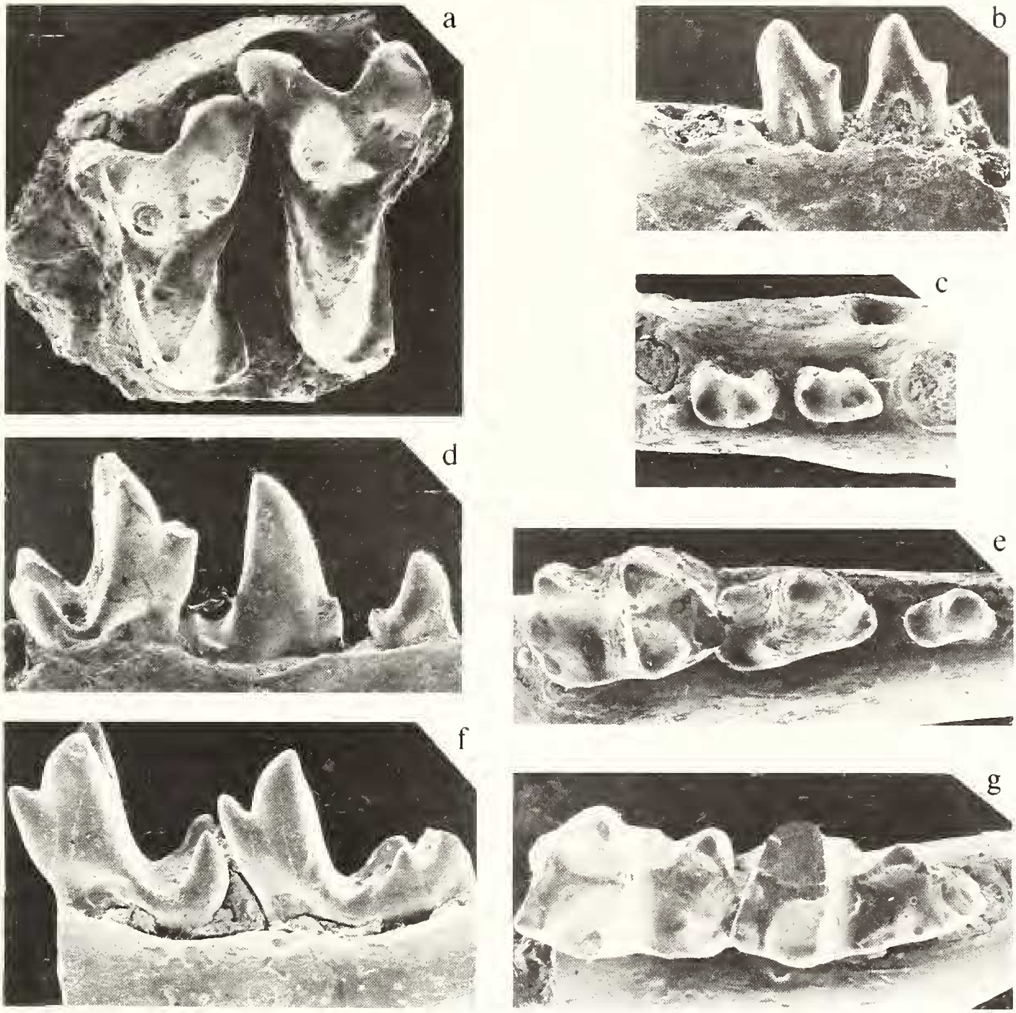
Etymology. Named after the Naran stream.

Naranius infrequens sp. nov.

Text-fig. 7*a–g*

Holotype. Specimen PSS 20-73, left mandibular fragment with P/3–M/1 and alveoli of P/1 and P/2.

Referred material. PSS 20-64, isolated right M/1; PSS 20-72, left mandibular fragment with P/2–P/3; PSS 20-75, left mandibular fragment with P/4–M/2; PSS 20-79, right mandibular fragment with M/3; PSS 20-81, left mandibular fragment with talonid of M/2 and M/3; PSS 20-82, left mandibular fragment with talonid of M/2 and M/3; PSS 20-83, right mandibular fragment with talonid of M/1 and damaged M/2; PSS 20-84, right mandibular fragment with damaged M/2 and M/3; PSS 20-90, right mandibular fragment with damaged M/2 and talonid of M/3; PSS 20-91, edentulous left mandibular fragment; PSS 20-93, right mandibular fragment with talonid of M/1, damaged M/2, and alveoli from posterior side of canine to anterior root of M/1; PSS 20-97, right mandibular fragment with M/2–M/3; PSS 20-105, left mandibular fragment with damaged M/2; PSS 20-106, left mandibular fragment with talonid of M/2 and M/3; PSS 20-109, right mandibular fragment with damaged M/2 and M/3; PSS 20-112, right mandibular fragment with talonid of M/2 and roots of M/3; PSS 20-113, right mandibular fragment with M/1 and damaged M/2; PSS 20-121, right mandibular fragment with P/4-M/2 (all without enamel).



TEXT-FIG. 7. *Naranius infrequens* gen. et sp. nov. *a*, PSS 20-126, left M1/M2/, occlusal view, ×20. *b* and *c*. PSS 20-72, left P/2–P/3; *b*, lingual view; *c*, occlusal view, ×20. *d* and *e*, PSS 20-73, left P/3–M/1, holotype; *d*, lingual view; *e*, occlusal view, ×20. *f* and *g*, PSS 20-97, right M/2–M/3; *f*, lingual view; *g*, occlusal view, ×20. All specimens are from Tsagan-Khushu, Naran-Bulak Formation, Bumban Member, MPR, and are housed in the Institute of Geology, Ulan Bator.

Locality and horizon. Tsagan-Khushu, Nemegt Basin, People's Republic of Mongolia; Naran-Bulak Formation, Bumban Member, Quarry I (PSS 20-64, PSS 20-72, PSS 20-75, PSS 20-79, PSS 20-81, PSS 20-82, PSS 20-83, PSS 20-84, PSS 20-105, PSS 20-106, PSS 20-109, PSS 20-112, PSS 20-113) and Quarry II (PSS 20-90, PSS 20-91, PSS 20-93, PSS 20-97).

Age and distribution. Early Eocene of the Naran-Bulak Formation at Tsagan-Khushu.

Diagnosis. As for genus.

Etymology. *infrequens*, Latin; rare.

Description. The mandible is long and low; mental foramina occur below the anterior border of P/2 and below the posterior part of P/4; the latter is much the smaller. The symphysis extends posteriorly to the level of P/2.

The alveoli of three incisors are preserved; all three teeth appear to have had about the same proclivity with I/2 apparently the largest. From the alveolus the canine was large and single rooted; a relatively large, single rooted P/1 closely followed it. P/2 and P/3 (text-fig. 7*b*, *c*) are considerably smaller than P/4 and apparently smaller than P/1. They are biradicular, subequal in size, and morphology with a small, unbasined talonid traversed medianly by a slight anteroposterior crest terminating posteriorly in a minute cusp. In orientation the premolars continue the vertical axis of the mandible, but the molars are tipped lingually; with respect to the vertical plane of the symphysis the premolars are tipped and the molars vertical.

P/4 (text-fig. 7*d*, *e*) is essentially a single cusped tooth; a minute paraconid occurs low on the crown and a metaconid is lacking. The dominant protoconid is moderately high and recurved. A posterolingual crest descends the protoconid but is not continued by the talonid crest. The latter, oriented slightly obliquely, divides the unbasined talonid into unequal parts and terminates in a moderately high median cusp.

In the molars (text-fig. 7*d–g*) the protoconid and metaconid are moderately high and are subequal. The anterior crest of the protoconid joins the labial base of the paraconid, with which it makes a flat angle. The paraconid is relatively high situated but is small and projects little anteriorly. The protoconid is posterior with respect to the metaconid. Cristid obliqua contact with the posterior trigonid wall is low. The talonid is slightly wider than the trigonid in M/1 and subequal in M/2. The hypoconid is the principal talonid cusp, with the large and medianly placed hypoconulid being only a little less high. The entoconid is the smallest of the three, but it is considerably higher than that of *Oedolius perexiguus*. It is situated at the posterolingual corner of the tooth, but being round it does not give the impression of being obliquely placed; it is slightly posterior with respect to the hypoconid. The talonid is deeply basined but lacks a lingual wall; a broad U-shaped notch separates the entoconid and the metaconid. M/3 is characterized by a long, narrow talonid, with no (or extremely little) lingual prominence of the entoconid.

The fragment of maxillary, PSS 20-126 (text-fig. 7*a*), containing M1/ and M2/ and two alveoli of P4/, might be a little large for attribution to *N. infrequens*, but it occludes fairly well and the teeth are of corresponding morphology. M1/ and M2/ are strongly transversely elongated and narrow anteroposteriorly lingual to the paracone and metacone. The latter are moderately high and slender and situated close together; the paracone is the bigger and higher of the two. It is unconnected with the parastyle, which in M1/ is directed anteriorly; strong transverse wear has eliminated details on the parastyle. In M2/ this style forms a large lobe, directed anterolabially; a simple cuspule crowns its occlusal surface. The metacone and metastyle are connected by a high crest that is slightly concave anterolabially in M1/; the stylar lobe, directed posterolabially, is devoid of cusps or cingula. In M2/ the lobe is directed more labially and the crest from the metacone is notched where it is joined by the postmetaconular crest (but in neither tooth is a deep notch developed in the metacrista as it is in *Cimolestes*). A deep, asymmetrical labial notch (ectoflexus) is formed between the stylar lobes. The paraconule is faintly developed, being little more than a minor elevation in the preprotocrista; a short, faint crest is visible at the base of the paracone, testifying to the probable former presence of a postparaconular crest. The metaconule is more prominent, but again, it is not cuspate and forms an elongate thickening in the postprotocresta; there is no trace of a premetaconular crista. The protocone is subequal in height to the paracone; in lingual view it is nearly vertical and in M2/ it even leans slightly posteriorly. A slight, but long basal precingulum is present as well as an even longer postcingulum; the latter develops a narrow shelf lingually, on which occurs, squaring the posterolingual corner, a cuspule.

From the two remaining alveoli, P4/ was as wide (transversely) as the anterior part of the first molar. Presumably, the two labial roots were widely spaced; indicating a rather triangular tooth.

Measurements.

		Length	Width
PSS 20-72:	P/2	0·5	0·35
	P/3	0·5	0·4
PSS 20-73:	P/3	0·5	0·3
	P/4	1·1	0·6
	M/1	1·4	0·85
PSS 20-106:	M/3	1·45	0·9
PSS 20-81:	M/3	1·5 est.	0·95
PSS 20-79:	M/3	1·55	0·9
PSS 20-84:	M/2	1·25	0.85
	M/3	1·5	0·85
PSS 20-113:	M/1	1·45	0·85
	M/2	1·45	0·85 est.

PSS 20-109:	M/2	1·2	1·2
	M/3	1·4	–
PSS 20-82:	M/3	1·5	0·95
PSS 20-64:	M/1	1·4 est.	0·85
PSS 20-75:	P/4	1·2	0·6
	M/1	1·2	0·8
	M/2	1·2 est.	0·85
PSS 20-97:	M/2	1·4	1·0
	M/3	1·55	1·0
PSS 20-126:	M1/	1·4	2·0
	M2/	1·25	2·2

Comparisons. Except for being less than half the size of the late Cretaceous *Procerberus formicarum* the lower molars of *N. infrequens* are quite similar. Less resemblance can be seen in the Cretaceous species of *Cimolestes* but *Batodon tenuis* (recently referred to the Geolabididae; Novacek 1976; Krishtalka and West 1979) is also similar and is of a comparable size; the latter differs in possessing a P/2 and P/3 more anteriorly inclined, P/4 with a small metaconid, M/1–M/2 with a larger but lower situated paraconid, an apparently weaker entoconid, and sometimes a V-shaped notch between the entoconid and the metaconid instead of an open U. The M/3 has a shorter talonid and a more prominent entoconid.

Among the early Tertiary forms the middle Palaeocene *Palaeoryctes puercensis* is too advanced morphologically, but a species from Silver Coulee (late Palaeocene) shows a little more similarity. Differences include premolar loss, P/3 bigger, P/4 with a relatively large and high situated paraconid, considerably higher trigonids, and M/3 with a shorter talonid. The relatively low crowned *N. infrequens* is not close to these forms.

Mention could be made of certain similarities in the type specimen of the middle Palaeocene *Avunculus*, but most of these can be regarded as familial in nature. The same comment can be made for *Thelysia* (late Palaeocene). None of the other forms presently classified as palaeoryctids shows a significant similarity to a closer degree. Palaeoryctidae from the late Palaeocene of Morocco were cited in preliminary note (Cappetta *et al.* 1978), but the lower molar illustrated seems to be better placed in the Nyctitheriidae.

Concerning Eocene taxa, a non-molariform P/4 prompted research among the Pantolestidae; *Bessoecetor diluculi* (sometimes referred to *Propalaeosinopa*) in particular possesses morphological aspects reminiscent of those found in *N. infrequens*, but general differences are too great for affinity. Closer similarity is present in the various species of *Centetodon*, especially in the lower molars; their trigonids are often much like those in *N. infrequens*, as is the feeble entoconid development on the talonid. The hypoconulid tends to be more lingual in position, however, and the P/4 more molariform. So far, nothing resembling the distinctive upper molars of the Geolabididae has been found in Mongolia; we prefer to regard *N. infrequens* as referable to the Palaeoryctidae. None of the described insectivores from China or elsewhere in Asia shows a relationship to *N. infrequens*.

Comparison of the possibly referable maxillary, PSS 20-126, reveals (as for the lower dentition) more similarity with late Cretaceous palaeoryctids than with younger forms. Also, as with the lower molars, *Cimolestes* resembles less our specimen than does *Procerberus*, having stronger conules, a slightly greater stylar shelf development, and a more pronounced notch (in labial view) in the metacrista. Anteroposterior narrowness of the upper molars lingual to the paracone-metacone is variable in both *Procerberus* and *Cimolestes*, but the latter tends to have more sharply pointed cusps and to be slightly more adapted for shearing. *N. infrequens* would be more like *Cimolestes* in this respect. Little is known of the upper molars of *Batodon*, but, like *N. infrequens*, they are more transversely elongate than in *Cimolestes* and *Procerberus*. They differ from those of *N. infrequens* in having stronger conules, a wider labial shelf, and a shallower ectoflexus in M2/. In all three Cretaceous genera variably developed anterior and posterior cingula are present; they are sometimes absent and sometimes form an uninterrupted shelf across the lingual side of the protocone. Although nothing corresponding exactly to the cuspule in the position of a hypocone (when is a hypocone recognizable?) in the upper molars of *N. infrequens* was noted in the genera in question, the morphology seen in *N. infrequens* is not surprising for a palaeoryctid.

The early Tertiary species of *Palaeoryctes* and *Cimolestes* differ considerably in upper molar characters, while the other palaeoryctids are even further removed (in the instances where the upper teeth are known, for example *Didelphodus*, *Acmeodon*, *Aaptoryctes*). Those of *Centetodon* differ in having a lower, less tubular paracone-metacone, stronger conules, a more developed labial shelf and, especially, by the progressive development of two lingual roots. Although a hypocone is lacking, a cuspule can sometimes develop at the lingual extremity of the posterocingulum in a fashion similar to that in *N. infrequens*.

Tsaganius gen. nov.

Type species. *Tsaganius amibiguus* n. sp.

Diagnosis. Dental formula ?-1-4-3. P/1 uniradicular. P/2 biradicular and small. P/3 almost as large as P/4. P/4 with anterocingulum well below level of paraconid; distinct paraconid reaching to about half the height of protoconid; strong metaconid nearly as high as protoconid; talonid not basined and traversed medianly by a crest terminating posteriorly in a large cusp. M/1 and M/2 relatively short and of approximately same length; M/3 longest; cusps high and slender; paraconid moderately high and small; strong anterocingulum; protoconid and metaconid subequal; no oblique groove on posterior surface of metaconid; cristid obliqua contact low on trigonid and labial with respect to the protoconid-metaconid notch; talonid relatively short; hypoconulid highest cusp with hypoconid slightly lower and entoconid lowest; entoconid situated at posterolingual corner of talonid, opposite hypoconid. M/3 with narrow talonid and short and moderately prominent hypoconulid.

Etymology. From *tsagan*, Mongol; meaning white.

Tsaganius ambiguus sp. nov.

Text-fig. 8*a*–*f*

Holotype. Specimen PSS 20-89, left mandibular fragment with talonid of P/4, M/1–M/3.

Referred material. PSS 20-67, right mandibular fragment with talonid of M/1, M/2–M/3, and alveoli of P/4; PSS 20-115, left mandibular fragment with P/4 and alveoli of P/1–P/3 and M/1–M/2.

Locality and horizon. Tsagan-Khushu, Nemegt Basin, People's Republic of Mongolia. Naran-Bulak Formation, Bumban Member, Quarry I (PSS 20-67, PSS 20-115) and Quarry II (PSS 20-89).

Age and distribution. Early Eocene of the Naran-Bulak Formation at Tsagan-Khushu.

Diagnosis. As for genus.

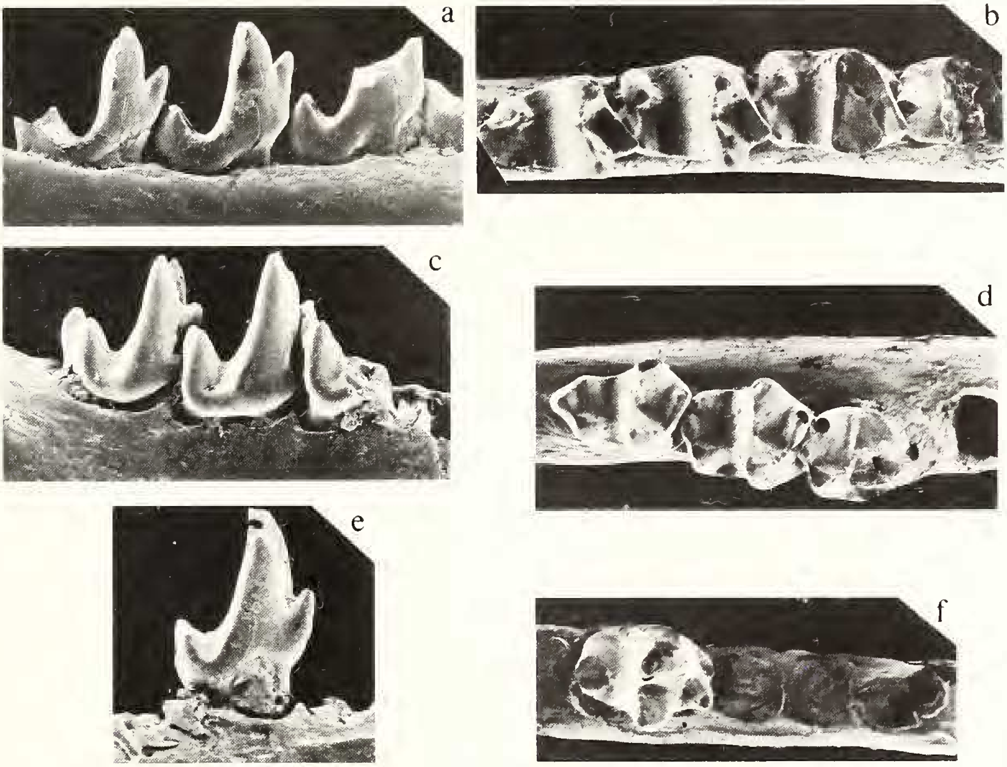
Etymology. *ambiguus*, Latin; meaning uncertain or enigmatic.

Description. The mandible is long and low; mental foramina occur below the posterior part of P/2 and below the anterior part, or middle of M/1. The symphysis extends posteriorly to the level of P/2. Only the alveoli of the anterior premolars are preserved; P/1 was apparently about the size of P/2 but possessed a single root; P/2, biradicular, was considerably smaller than P/3, which was apparently nearly as big as P/4.

Lacking the entire row of alveoli one cannot, of course, be certain of the identity of the teeth that occupied those that remain. The above interpretation is, we think, the most probable, but in the case where the most anterior preserved alveolus would be that of the canine we would suppose that the P/1 is lost; the two small alveoli that follow almost certainly belong to a two-rooted tooth and this tooth would be P/2.

P/4 (text-fig. 8*e*, *f*) has a well-developed trigonid with a distinct paraconid that is nearly vertical in orientation. Like all the trigonid cusps (and those of the molars) it is slender and approaches a tubular aspect. In height it probably equalled that of the hypoconulid (which is damaged in PSS 20-115), reaching to about halfway up the protoconid. A short but distinct anterocingulum occurs labial with respect to the paraconid and well below it. The talonid is rather short and the terminal cusp (preserved in the holotype) is a large, high cusp fitting snugly between the anterior cingulum and the base of the paraconid of M/1. The anteroposterior crest traversing the talonid is rather low and divides it into unequal parts.

In the molars (text-fig. 8*a–d*) the paraconid and metaconid are of subequal size, but the posteromedian crest of the metaconid is characterized by a slight concavity in unworn specimens (visible in anterior or posterior view). The anterior crest of the protoconid forms a nearly straight line with the crest of the paraconid;



TEXT-FIG. 8. *Tsaganius ambiguus* gen. et sp. nov. *a* and *b*, PSS 20-89, left talonid of P/4, M/1–M/3, holotype; *a*, lingual view; *b*, occlusal view, ×20. *c* and *d*, PSS 20-67, right talonid of M/1, M/2–M/3; *c*, labial view; *d*, occlusal view, ×20. *e* and *f*, PSS 20-115, left P/4; *e*, lingual view; *f*, occlusal view, ×20. All specimens are from Tsagan-Khushu, Naran-Bulak Formation Bumban Member, MPR, and are housed in the Institute of Geology, Ulan Bator.

as the crests connecting the protoconid and metaconid form an even straighter line, the trigonid in occlusal view forms a distinctive narrow V in contour. The paraconid is moderately high, relatively small, and projects little anteriorly. The paraconid and metaconid are opposite each other. Cristid obliqua contact with the posterior trigonid wall is low. Talonid–trigonid widths are subequal in M/1; the talonid is slightly the narrower in M/2. The hypoconid is relatively small, although remaining the principal talonid cusp in volume; the medianly placed hypoconid is slightly higher, however. The entoconid is small and barely cuspate; in occlusal view it terminates a straight crest from the hypoconulid and is situated opposite the hypoconid. A fairly wide U-shaped notch separates the entoconid and the metaconid. The talonid of M/3 is narrow but only a little longer than those of the preceding molars. Its minute and nearly crestiform entoconid produces a bulge in the lingual border of the talonid and maintains, with the moderately prominent hypoconulid, a straight connecting crest.

The P/4 and the molars are tipped lingually with respect to vertical axis of the mandible.

Measurements.

		Length	Width
PSS 20-67:	M/2	0·9	0·65
	M/3	0·9	0·65
PSS 20-89:	M/1	1·0	0·7
	M/2	0·95	0·73
	M/3	1·03	0·6
PSS 20-115:	P/4	0·95	0·6

Comparisons. At first glance *Tsaganius* appears quite close to *Naranius*, but detailed examination reveals a large number of distinctive characters. The difference in size of P/2 and P/3 and the tricuspid trigonid of P/4 are immediately notable. The molars differ less, but the anteroposteriorly narrow, symmetrically sided V of the trigonid occlusal surface, and its more slender cusps are noteworthy; on the talonid the high hypoconulid and the weaker entoconid also constitute differences, and the M/3 talonid is shorter and less linear lingually. The far posterior position of the posterior mental foramen is unusual in insectivores (cf. *Thelysia* Gingerich, 1982, a possible palaeoryctid), although typical of Pantolestidae.

Among the Cretaceous palaeoryctids, *Batodon* furnishes the most similarities, but differs in having P/2 and P/3 of subequal length, in lacking an anterocingulum on P/4, in possessing a definite angulation at the junction of the anterior protoconid crest and the paraconid crest, and a larger talonid; in M/3 the talonid is both longer and wider with a strong notch between the entoconid and the hypoconulid. Nevertheless, its small size, its slender trigonid cusps and molar talonid configuration, and the comparable molariform state of its P/4, lead one to envisage a similar sort of ancestor for *Tsaganius*. There are no described intermediate forms from the Palaeocene; in fact, we know of no other taxon that approaches so closely the dental morphology (as it is known today) of *T. ambiguus*.

Family PANTOLESTIDAE Cope, 1884, gen. indet.

Text-fig. 9*a*

Material. PSS 20-95, isolated right upper M1/ or M2/ (probably the latter); from Quarry II, Tsagan-Khushu.

This isolated tooth is much larger than those of the insectivores described above and breakage coupled with its disassociated state has hindered its analysis.

PSS 20-95 (text-fig. 9*a*) is little worn and moderate in transverse elongation with respect to its anteroposterior diameter. The summit of the paracone is broken but it was probably higher than the metacone. The two cusps are joined at their base, but, from the lingual base of the metacone, they are connate only to about midway on this cusp. Both paracone and metacone are relatively low and support strong anterior and posterior crests, the former extending to the parastyle and the latter to the metastyle. There is no notch in this metastylar wing separating it from the metacone; an elongage wear facet, extending along its length and pinching out near the summit of the metacone, indicates its use as a shearing surface. The metacone, in fact, is compressed labiolingually; it is oriented sub-vertically. The paracone is more inflated and slopes more abruptly labially. A moderately wide labial shelf exists labial to the metacone but it was probably very reduced opposite the paracone (the area is broken away). The metastyle is directed posteriorly and not at all labially. Little can be said of the shape of the parastyle, except that it probably did not extend farther anteriorly beyond its present state. The paraconule is higher, bigger, and more lingually situated than the metaconule; the preparaconular crest connects with the tip of the parastyle; a postparaconular crest is absent and there is no linkage with the paracone. The metaconule is more crestiform and possesses a strong premetaconular crest that is directed anterolabially to the lingual groove separating the bases of the paracone and metacone. The postmetaconular crest is strongly developed and extends to below the posterior side of the metacone; it does not follow the base of the metastylar wing. Loss of the protocone area is unfortunate. The anterior cingulum is slight and reaches to below the front of the paraconule. A hypoconal shelf and a strong hypocone are developed posteriorly. The tooth is moderately indented posteriorly at the end of the hypoconal shelf, and anteriorly about midway between the paraconule and the parastyle.

Measurements.

		Length	Width
PSS 20-95:	M2/?	4·9 est.	6·0 est.

Comparisons. In view of the incomplete nature of the tooth, identification can only be approximate. However, PSS 20-95 is of comparable size to North American *Palaeosinopa* and displays a morphology that is significantly similar. Gingerich (1980) pointed out that the two principal differences separating the late Palaeocene *Palaeotomus* from the late Palaeocene species of *Palaeosinopa* (*P. dorri*) lay in the greater anteroposterior width of the lingual part of M1/ in *Palaeosinopa* and a more labial position of the hypocone. These features in PSS 20-95 show a probable resemblance (the area is damaged) to *Palaeosinopa* in hypocone position and a lingual width that is about intermediate between the two. These observations suggest a closer affinity to *Palaeosinopa* than to *Palaeotomus*, which is also consistent with the age of Tsagan-Khushu; apart from *Palaeosinopa dorri*, *Palaeosinopa* is a typical early Eocene form.

PSS 20-95 is longer anteroposteriorly than the comparable tooth of *P. dorri* (metastylar development especially is greater), but is less elongate transversely. The known teeth of *P. dorri* are in an advanced stage of wear and it is not possible to compare paracone and metacone formation. The labial cingulum, however, is more marked and there seems to be no sharp premetaconular crista in the *P. dorri* M2/. Wasatchian material referred to *Palaeosinopa* is extremely variable as regards details. In specimens referred to *P. veterrima*, for example, the hypocone is strong on one specimen and absent on another; the premetaconular and postmetaconular crests are sharp and well defined on one and vague or absent on another; stylar and cingular development is also variable. In other specimens the paraconule is weaker than the metaconule, instead of the reverse, and the lingual width of a given tooth varies. This situation negates excessive reliance on particular details and renders necessary considerable caution when working with incomplete or inadequate samples. It is nevertheless possible to say that the basic morphology of PSS 20-95 resembles that of *Palaeosinopa* more than that of any other genus known to us.

In Europe the upper teeth of *P. osborni*, from the Ypresian of France, have not yet been studied, the later Eocene *Cryptopithecus* and *Dyspterna* are quite different and the middle Eocene *Buxolestes* lacks any development of a shearing metastyle; but *Pagonomus* (late Palaeocene) shows a metastylar flare quite similar to that of PSS 20-95. However, the paracone and metacone are less connate and the tooth of less massive aspect.

The diminutive pantolestid from the late Palaeocene of North America, *Bessoecetor* (or *Propalaeosinopa*), should be cited for the size and shape of its upper molar metastyle, thereby constituting another link between PSS 20-95 and this group. It is not as similar as *Pagonomus*, however.

The wide flaring of the metastyle in PSS 20-95, more than in typical *Palaeosinopa*, might indicate a generic difference, as might the basally connate paracone and metacone. But the latter are found to an even greater degree in a specimen from Bear Creek (AMNH 22221), referred to *P.* cf. *didelphoides*. For the moment, it is not possible to go further than a designation of Pantolestidae gen. indet. for PSS 20-95, while keeping in mind an intriguing similarity with *Pagonomus* and an affinity with *Palaeosinopa*.

An isolated left lower M/3, PSS 20-128 (text-fig. 9*g*, *h*), from Quarry I might be referable to the same taxon as PSS 20-95. It is of comparable size; the trigonid is moderately high and supports a well excavated trigon basin. The paraconid is large, high, and crestiform and is separated from the anterior protoconid crest by a deep notch; another notch occurs between the median crests of the protoconid and metaconid. The latter is only slightly higher than the paraconid, while the protoconid is by far the highest cusp. Vertically, along its posterolingual border, the metaconid is inflated into a rounded ridge. The talonid is of moderate proportions (approximately the same length as the trigonid); the hypoconid is the highest cusp and forms a strong V labially in occlusal view. The hypoconulid is a cusp nearly as big, projecting posteriorly. By far the smallest of the three talonid cusps is the entoconid, crestiform and situated opposite the hypoconid. The anterior crest of the entoconid is parallel to the cristid obliqua and both are oriented posterolabially. The cristid obliqua contacts the posterior trigonid wall below the notch.

Following the apparent affinity deduced for the upper molar, PSS 20-95, the relationships of PSS 20-128 also appear to lie within the Pantolestidae. Comparison with specimens of *Palaeosinopa* from Bitter Creek, Wyoming, and of *P. incerta*, both Wasatchian, shows a particular similarity (see

TEXT-FIG. 9. *a*, Pantolestidae gen. indet., PSS 20-95, right M1/ or M2/, occlusal view, ×10·5. *b* and *c*, Nyctitheriidae gen. indet., PSS 20-70, partial left M/1 or M/2; *b*, lingual view; *c*, occlusal view, ×15. *d* and *e*, cf. *Hyracolestes* sp., PSS 20-124, left M/1 or M/2; *d*, occlusal view; *e*, lingual view, ×15. *f*, Nyctitheriidae gen. indet., PSS 20-60, right M1/, occlusal view, ×15. *g* and *h*, Pantolestidae gen. indet., PSS 20-128, left M/3; *g*, lingual view; *h*, occlusal view, ×10. All specimens are from Tsagan-Khushu, Naran-Bulak Formation, Bumban Member, MPR, and are housed in the Institute of Geology, Ulan Bator.

Bown and Schankler (1982) for an excellent discussion of the latter and other early insectivores). Minor differences include: the talonid cristid obliqua and the anterior crest of the entoconid are oriented less posterolabially, the talonid basin is a little wider, the metaconid has less of a vertical bulge posteriorly, and the paraconid is smaller.

In some creodonts the trigonid cusps have a similar aspect, although they tend to be more inflated. Usually the cristid obliqua is directed more anteroposteriorly, the hypoconid does not project labially and forms a massive crest, the talonid basin is deeper, and the region containing the entoconid and hypoconulid is diversely modified but in no way closely resembles that seen in PSS 20-128. The supposition that this tooth belongs to the same taxon as PSS 20-95 is supported by the evidence available, but proof, of course, is lacking.

Another isolated lower molar, PSS 20-63, entirely lacks enamel. It appears to have had a morphology similar to that of PSS 20-128 described above, but nothing of decisive value can be deduced from it.

Order indet.
Family indet.
cf. *Hyracolesties* sp.

Text-fig. 9*d*, *e*

Material. PSS 20-124, isolated left lower M/1 or M/2, from Quarry I, Tsagan-Khushu.

This tooth (text-fig. 9*d*, *e*), excellently preserved, represents an animal with a largely carnivorous diet. The trigonid is high with a wide, lingually open basin. The paraconid is large, high, and crestiform and is separated from the anterior crest of the protoconid by a marked notch. A vertical crest occurs at its most anterior point. The protconid is by far the highest of the trigonid cusps and slopes dorsolingually so that (in posterior view) its tip is situated in line with the hypoconulid. The metaconid is well below the protoconid but is higher than the paraconid. A notch occurs at the midline between the median crests of the metaconid and protoconid. A strong anterocingulum crosses obliquely the base of the protoconid and extends posteriorly on the lingual base of the cusp. The talonid is narrow but nearly as long as the trigonid. While constituting the principal talonid cusp the hypoconid is small with little labial projection; the cristid obliqua is only moderately oriented anterolingually and contacts the posterior wall of the trigonid well below the notch. The hypoconulid is large, nearly as big as the hypoconid and is as high. The entoconid is a little lower, is situated slightly posterior with respect to the hypoconid, and is crestiform. Its anterior crest (parallel the cristid obliqua) closes the deep talonid basin except just behind the metaconid. A strong posterocingulum extends from the tip of the hypoconulid labially to below the hypoconid, forms a sharp angulation (in occlusal view) at the posterolabial corner of the tooth, and nearly meets the posterior extension of the anterocingulum.

Measurements.

	Length	Width
PSS 20-124: M/1 or M/2	2·6	1·5

Comparisons. PSS 20-124 is close in size to *Bumbanius rarus* but it differs markedly by its narrower talonid, by its higher paraconid, and the presence of a notch between the latter and the protoconid. It is quite different from the other insectivores known at Tsagan-Khushu.

The carnivorous aspect of the tooth prompted comparison first of all with the Hyaenodontidae, but talonid details are unlike any seen in that group. The M/1 of miacids was also examined. Usually the trigonid in these forms is lower and more inflated. The talonid is usually shorter and the size and disposition of the talonid cusps is different. *Simpsonictis tenuis* (middle Palaeocene, North America) is the closest in morphology, but its talonid is distinctly wider. A labial cingulum is present, however, as in PSS 20-124.

While certainly not identical the M/1 of *Hyracolestes ermineus* bears some resemblance to PSS 20-124. Unlike the preceding forms it is about the same size. The trigonid cusps are of similar proportions, although the protoconid is less inflated lingually and does not seem to slope dorsolingually (but the summit of the cusp is lacking in the holotype). The talonid is also of similar proportions but the hypoconid has been broken off and the entoconid worn off, which inhibits a precise comparison. No cingula are present on the holotype of *Hyracolestes*; even the presence of an anterocingulum is unsure as the area is worn. A referred specimen of *Hyracolestes* from the upper part of the Doumu Formation (Qianshan Basin, Anhui Province, China) is poorly preserved and shows little that is not indicated on the type. The remains of an anterocingulum occur, however.

The relationships of PSS 20-124 are far from clear. For the moment it is not possible to refer it to either a family or to a known genus. There is a possibility that it might be related to *Hyracolestes*, but more complete material of both are needed. Except for the resemblance seen in *Simpsonictis* it is not likely that PSS 20-124 is related to the Miacidae and it surely bears no affinity to the Hyaenodontidae.

CONCLUSIONS

For the most part relatively minor details separate *Bumbanius* and *Leptacodon*, although differences indicating generic distinction do exist (entoconid and hypoconulid size and relations, in particular). Excepting, principally, the placement of the paraconid in the known teeth of *Praolestes*, there is sufficient similarity between it and *Bumbanius* to suspect the existence of a common relationship within the Nyctitheriidae.

Oedolius shows a closer relationship to *Bumbanius* than to any other known genus and the two together suggest the presence in Asia of a group that is still undefined. Additional material may someday provide evidence for new suprageneric taxa to include the slowly accruing material and knowledge of Asiatic insectivores, but for the moment we will content ourselves with assignment of *Bumbanius* and *Oedolius* to the Nyctitheriidae.

Two specimens (PSS 20-62 and PSS 20-60), consisting of upper teeth, testify to the diversity of lipotyphlan insectivores in the Tsagan-Khushu fauna, but they have been left unnamed.

The greatest similarity to *Naranius* among existing taxa is to be found among the late Cretaceous Palaeoryctidae of North America, *Procerberus* and *Batodon*, in particular. Whether or not these, or closely related genera, inhabited Asia in the Cretaceous is not yet demonstrated. It would appear, however, that *Naranius* is a primitive, relatively low-crowned descendant of stock that was dentally closely similar to them. Given the lack of evidence from the Palaeocene of Asia it is not possible to speculate profitably on the point of origin of *Naranius*'s ancestors. The same must be said for *Tsaganius*, with even more emphasis on the apparent relationship it shares with *Batodon*.

The pantolestid specimen, from what can be deduced of its morphology, suggests affinity with late Palaeocene and Eocene North American and European forms.

In summary, it should be noted that the new insectivores from the early Eocene of Mongolia do not show signs of particularly strong endemism. Quite the contrary, they uniformly indicate a relationship to North American late Cretaceous or late Palaeocene forms. To what extent this translates the intercontinental exchange that produced the appearance of Wasatchian/Ypresian Holarctic genera such as *Hyracotherium* and *Hyopsodus*, or how much is due to previous exchange cannot yet be determined. Whatever the moment of dispersal, it is clear to us that the taxa described here are rather closely related to others in North America and Europe and did not develop in isolation.

The principal aim of these descriptions is to put the taxa on record and available for discussion. It is too early for a coherent taxonomy of the Eocene insectivores of Asia.

Acknowledgements. The authors would like to express their appreciation to Dr T. M. Brown and Professor P. D. Gingerich for having read the manuscript and considerably improved it by their judicious remarks. Dr P. M. Butler examined the specimens after the manuscript was written and kindly sent extensive comments. Our conclusions are, for the most part, concordant. The figures were drawn by Mesdemoiselles J. Crapart and S. Vrain, the SEM photos taken by Madame C. Weber, and the manuscript typed by Madame S. Guignès.

REFERENCES

BOWN, T. M. and SCHANKLER, D. 1982. A Review of the Proteutheria and Insectivora of the Willwood Formation (lower Eocene), Bighorn Basin, Wyoming. *Geol. Surv. Bull.* **1523,** i–iv, 1–79.

CAPPETTA, H., JAEGER, J. J., SABATIER, M., SIGE, B., SUDRE, J. and VIANEY-LIAUD, M. 1978. Découverte dans le Paléocène du Maroc des plus anciens mammifères euthériens d'Afrique. *Geobios*, **11** (2), 257–262.

DASHZEVEG, D. 1976. Novyye mezonikhidy (Condylarthra, Mesonychidae) iz paleogena Mongolii (New mesonychids (Condylarthra, Mesonychidae) from the Palaeogene of Mongolia). *In* KRAMARENKO, N. N. (ed.). *Paleontologiya i biostratigrafiya Mongolii, Sovmestnaya Sov.—Mong. Paleont. Eksped.* **3,** 14–31. [In Russian.]

—— 1977. O pervoy nakhodye *Hyopsodus* Leidy, 1870 (Mammalia, Condylarthra) v Mongol′skoy Narodnoy Respubliye (On the first occurrence of *Hyopsodus* Leidy, 1870 (Mammalia, Condylarthra) in the People's Republic of Mongolia). *In* BARSBOLD, R (ed.). *Fauna, flora i biostratigrafiya mezozoya i kaynozoya Mongolii. Sovmestnaya Sov.—Mong. Nauchno-Issled. Geol. Eksped.* **4,** 7–13 [In Russian.]

—— 1979*a*. Nakhodka girakoteriya v Mongolii (Discovery of a hyracothere in Mongolia). *Paleontol. Zh.* **3,** 108–113. [In Russian].

—— 1979*b*. Nakhodka Homogalax (Perrisodactyla, Tapiroidea) v Mongolii i ego stratigraficheskoye znacheniye (A find of *Homogalax* (Perissodactyla, Tapiroidea) in Mongolia and its stratigraphic significance). *Byulletin Moskovskogo Obshchestva Ispytateley Prirody, Otdel Geol.* **54** (6), 105–111. [In Russian.]

—— 1982. La faune de Mammifères du Paléocène inférieur de Naran-Bulak (Asie Centrale) et ses corrélations avec l'Europe et l'Amérique du Nord. *Bull. Soc. Géol. Fr.* (7), **24** (2), 275–281.

—— and MCKENNA, M. C. 1977. Tarsioid Primate from the early Tertiary of the Mongolian People's Republic. *Acta. Palaeont. Polonica*, **22** (2), 119–137.

GINGERICH, P. D. 1980. A new species of *Palaeosinopa* (Insectivora; Pantolestidae) from the late Paleocene of Western North America. *J. Mamm.* **61** (3), 449–454.

—— 1982. *Aaptoryctes* (Palaeoryctidae) and *Thelysia* (Palaeoryctidae?): new insectivorous mammals from the late Paleocene and early Eocene of Western North America. *Contrib. Mus. Paleont., Univ. Michigan.* **26** (3), 37–47.

GRADZINSKI, R., KAZMIERCZAK, J and LEFELD, J. 1969. Geographical and geological data from the Polish–Mongolian Palaeontological Expeditions. Results Polish–Mongol. Palaeont. Exped. I. *Palaeont. Pal.* **19,** 33–82.

KRISHTALKA, L. and WEST, R. M. 1979. Paleontology and geology of the Bridger Formation, southern Green River Basin, southwestern Wyoming, Part 4. The Geolabididae (Mammalia, Insectivora). *Contrib. Biol. Geol., Milwaukee Pub. Mus.* **27,** 1–10.

NOVACEK, M. J. 1976. Insectivora and Proteutheria of the later Eocene (Uintan) of San Diego County, California. *Contrib. Sci., Nat. Hist. Mus., Los Angeles Co.* **283,** 1–52.

SZALAY, F. S. and MCKENNA, M. C. 1971. Beginning of the age of mammals in Asia: the late Paleocene Gashato fauna, Mongolia. *Amer. Mus. Natur. Hist., Bull.* **144** (4), 269–318.

D. E. RUSSELL
Institut de Paléontologie
UA 12 CNRS
8, rue Buffon
75005 Paris, France

D. DASHZEVEG
Institute of Geology
Academy of Sciences
Ulan Bator,
Mongolian People's Republic

Typescript received 25 January 1985
Revised typescript received 22 July 1985